Adaptations among Palcozoic Insects

F. M. CARPENTER
Harvard University, Cambridge, Mass. 02138

INTRODUCTION

Although our knowledge of Paleozoic insects is still largely based on wings, information about their body structures is now being acquired to a much greater extent than previously. While this is due in part to discovery of new insect deposits which give exceptionally fine details of preservation, restudy of specimens collected and originally described many years ago has contributed equally. The insects collected more than fifty years ago, in the Upper Carboniferous shales of Commentry in France, for example, have only recently been subjected to intensive and careful examination. As might well have been expected, the body structures of Paleozoic insects that are now known require many changes in our understanding of the nature and relationships of the species concerned. What is most notable, however, is the degree of specialization, especially of adaptive structures, that insects had clearly attained by the end of the Paleozoic. In the following account, I have brought together some examples of adaptive modifications that have been found in Upper Carboniferous and Permian insects.

MAIN LINES OF INSECT EVOLUTION

As preliminary background for this discussion, I summarize here the present concept of the main lines of insect evolution. This envisions the Class Insecta as being monophyletic, derived from terrestrial arthropod stock that resembled machilid thysanurans but with functional, abdominal legs. The insect line began with primitively wingless types, perhaps not very different from thysanurans; all of these, including the Recent Thysanura, constitute the subclass Apterygota. From such ancestors, probably in the early part of Lower Carboniferous times, winged insects arose. Most of the evidence now obtainable supports the concept, at least as a working hypothesis, that the winged insects constitute a monophyletic line, comprising the subclass Pterygota.

A few wingless species occur in nearly all of the orders included in this subclass, but they are, of course, secondarily apterous. Studies based on both fossil and existing insects indicate that the earliest winged insects had a restricted wing articulation, preventing the wings from being folded back over the body when the insect was not in flight. At the present time, there are two orders of insects, the mayflies and the dragonflies, that are in this category, but at least four other orders existing in the Paleozoic apparently belonged here. This series of insects comprises that division of the Pterygota known as the Paleoptera or ancient-winged insects.

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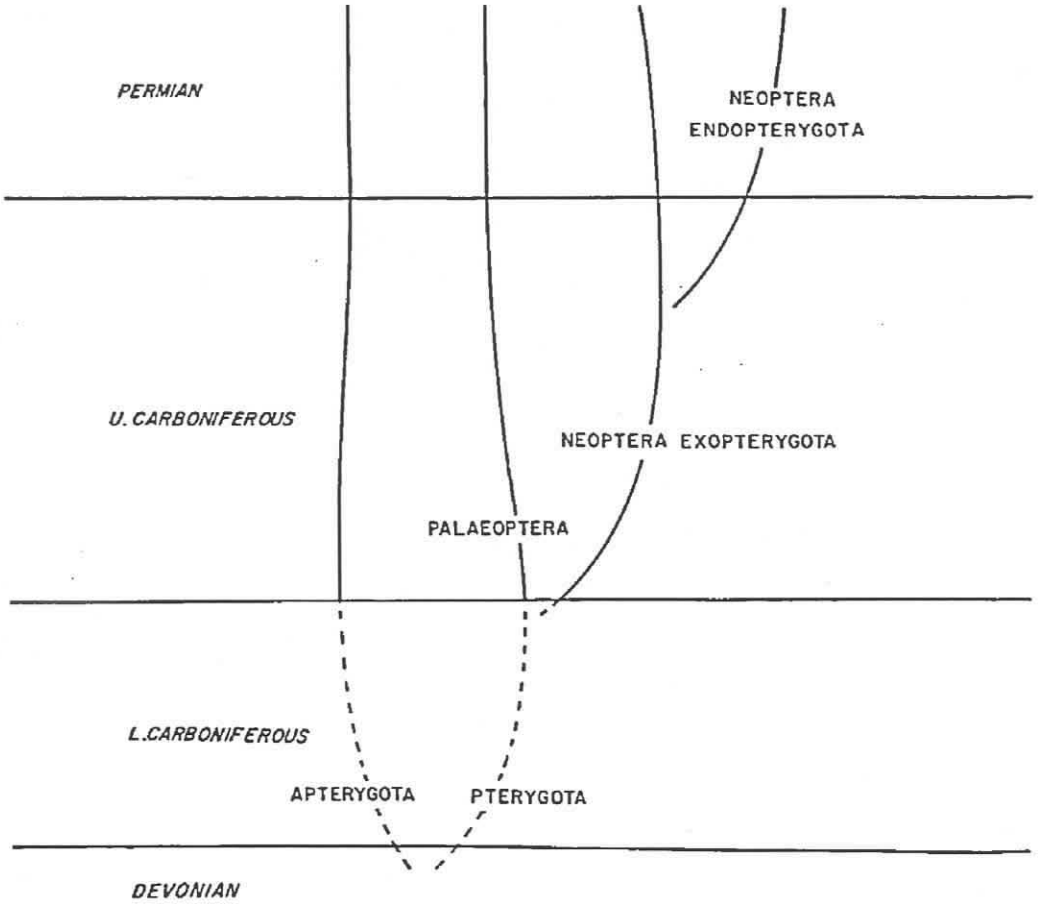


FIG. 1. Diagram of the main lines of insect evolution, based on the concept of Martynov (1938).

At some time prior to the Upper Carboniferous, the insects developed a line which had a very different method of wing articulation, one that permitted flexing of the wings back over the body in the resting state; this was accomplished by development of a special plate in the wing base (the third axillary) and muscles which controlled it. All the remaining orders of winged insects belong to this complex, which is known as the Neoptera. Study of the more primitive members of the Neoptera shows that they have a post-embryonic development in which the immature forms resemble the adults in general form, feed upon the same type of food as the adults and live in the same environments; these are Exopterygote Neoptera. From this group there developed another line, also monophyletic so far as we are aware, this being the insects in which the post-embryonic stages—the larvae—differ in appearance from the adults, feed upon different food from that of the adults and occupy different environments; these are the Endopterygote Neoptera.

This concept of insect evolution is one which was originally proposed by Dr. A. V. Martynov of the Soviet Academy of Sciences (1925; 1938); it

cannot be considered a proven concept but it is a working hypothesis which seems to fit the evidence as we now know it better than any other model that has been advanced. The bearing of this on a discussion of adaptations among Paleozoic insects becomes obvious if we superimpose this phylogenetic concept on the geologic time scale (Fig. 1). Several orders of Recent, endopterygote insects [Neuroptera (Plannipennia), Raphidiodea, Trichoptera and probably Coleoptera] are known from as far back as middle Permian time, and the endopterygote line presumably developed by the end of the Pennsylvanian (Upper Carboniferous); since several orders of neopterous insects are known from the earliest horizon (Namurian) of the Upper Carboniferous, the exopterygote line must have arisen before the end of the Lower Carboniferous. There are no remains of true insects in deposits prior to Upper Carboniferous, but we can only conclude that the paleopterous insects existed before then and the apterygotes even earlier, perhaps as far back as the Devonian.

The Collembola, of which there is a Devonian record, are not included in this discussion since they are clearly not of the same phylogenetic complex as the Apterygota and Pterygota and are in fact recognized as outside the Class Insecta. I have also excluded from this account *Eopterum devonicum* Rohdendorf from the Devonian of the Soviet Union; I am not convinced from my examination of the unique specimen on which the species is based that it is an insect.

It is apparent, therefore, that the three great stages in insect evolution (development of wings, of wing-flexing, and of complicated post-embryonic development) took place before the end of the Upper Carboniferous. That the Paleozoic insects had great diversity of structure is not surprising in view of this long history. In the accompanying diagram (Fig. 1) I have summarized the main evolutionary lines but for the sake of simplicity I have not attempted to indicate the positions of any orders. The orders Palaeodictyoptera, Megasecoptera and Diaphanopterodea, which will be mentioned frequently in the following discussion, are members of the paleopterous line, occurring in the Upper Carboniferous and Permian; the Blattaria (cockroaches) and Orthoptera are neopterous-exopterygotes, ranging from Upper Carboniferous to the present; the Protorthoptera are also exopterygotes, known only from the Upper Carboniferous and Permian; the Protelytroptera are exopterygotes, known definitely only from the Permian; and the Hemiptera are exopterygotes occurring from Permian to the present.

MOUTH PARTS

A very interesting feature of the Palaeodictyoptera, Megasecoptera and Diaphanopterodea that has been discovered in recent years is the presence of piercing-sucking mouthparts. Actually, structures which we now realize were parts of the sucking beak were observed in the Palaeodictyoptera nearly

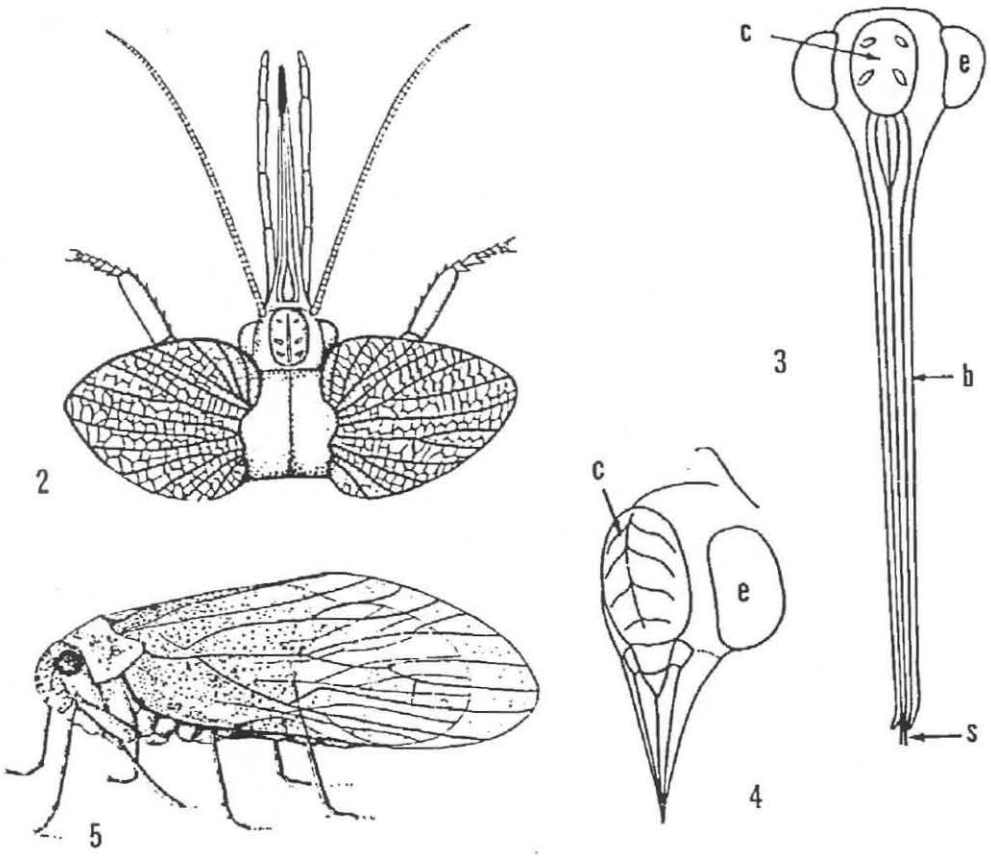


FIG. 2. Drawing of the head and prothorax of *Stenodictya lobata* Brongniart (Palaeodictyoptera), from Upper Carboniferous shales of Commentry, France; from an original drawing by Dr. J. Kukalová, based on specimens in Institut de Paléontologie, Paris (see also Kukalová, 1970a). The head is represented in a prognathous position in order to show the beak.

FIG. 3. Drawing of frontal view of head of *Mecynostoma dohrni* (Brongniart) (Palaeodictyoptera), from Upper Carboniferous shales of Commentry, France; original drawing by Dr. J. Kukalová, based on type specimen in Institut de Paléontologie, Paris (see also Kukalová, 1970a). c, clypeus; e, compound eye; b, beak; s, stylets.

FIG. 4. Drawing of oblique-frontal view of head of *Asthenohymen dunbari* Tillyard (Diaphanopterodea), from Lower Permian of Kansas; original drawing by Dr. J. Kukalová, based on specimens in Museum of Comparative Zoology.

FIG. 5. Drawing of *Permocicada integra* Becker-Migdisova (Hemiptera); based on specimens from Permian deposits of Iva Gora, USSR (from Becker-Migdisova, 1962).

a century ago but they were interpreted as antennae. One Permian specimen, described as *Eugereon* at about the beginning of this century, had the mouthparts as well as the antennae very clearly preserved; the specimen obviously had a long, sucking beak but because only the bases of the wings were preserved, the true affinities of this insect were not obvious and it was placed in a separate order, Protohemiptera, regarded as ancestral to the existing Hemiptera.

However, restudy in recent years of the remarkably preserved Palaeo-

dictyoptera in the Commentry shales of France (Kukalová, 1969; 1970a; 1970b) as well as the examination of new material from the Permian of Kansas (Carpenter) and the Permian of the Soviet Union (unpublished) has shown that all Palaeodictyoptera, from the Spilapteridae to the Dictyoneuridae, had this sucking beak (Figs. 2, 3). Furthermore, it has become obvious from recently collected material that the Megasecoptera as well as the Diaphanopterodea had similar beaks (Fig. 4). Preservation of some of these specimens is so extraordinary that even the fine, piercing stylets within the beak itself can be distinguished; furthermore, the clypeal region of the head shows the same external modifications as it does in the existing Hemiptera, that is, an enlargement of the clypeal region to which the muscles that operate the sucking mechanism are attached, and the presence of transverse ridges that give support to the clypeal wall.

The size of the beaks was obviously very diverse in the Palaeodictyoptera and probably also in the Diaphanopterodea and Megasecoptera, as indicated in the accompanying figures. The position of the head in members of these orders was apparently very different from that in the Hemiptera. In the latter (Fig. 5) the head is so oriented that the beak extends somewhat posteriorly beneath the head and even under part of the thorax. It is virtually impossible for the hemipterous head to be held in such a way that the beak projects anteriorly. Most of the specimens of Palaeodictyoptera are preserved with the beak extended anteriorly, as represented in Fig. 2. However, it is probable that these insects fed with the mouthparts in a more nearly ventral or hypognathous position than the usual preservation indicates.

There can be no question that beaks in the Palaeodictyoptera and the other two orders mentioned were used for piercing and for sucking liquid nutriment. What the types of food were, we have no way of knowing; presumably they were of plant origin. The most likely sources were probably some of the succulent lycopods that were extensive and abundant during the Carboniferous and Permian.

In this connection, the diversity and striking development of true hemipterous insects with piercing-sucking mouthparts in the Permian period is certainly significant. Although not definitely known from the Upper Carboniferous, they are well represented in all levels of the Permian. These Permian forms belonging to the suborder Homoptera had the sucking beak as well developed as it is in the living species, so far as we can determine from the fossils. The best known of these Permian specimens are from several deposits in the Soviet Union. One of these shown in Fig. 5 is based upon many specimens that have the structural details clearly preserved (Becker-Migdisova, 1962). From study of such fossils it is obvious that the clypeal region (postclypeus) was enlarged and modified in connection with the sucking apparatus, as in Recent Hemiptera. The diversity of Homoptera in Permian times was truly extraordinary; these represent a wide

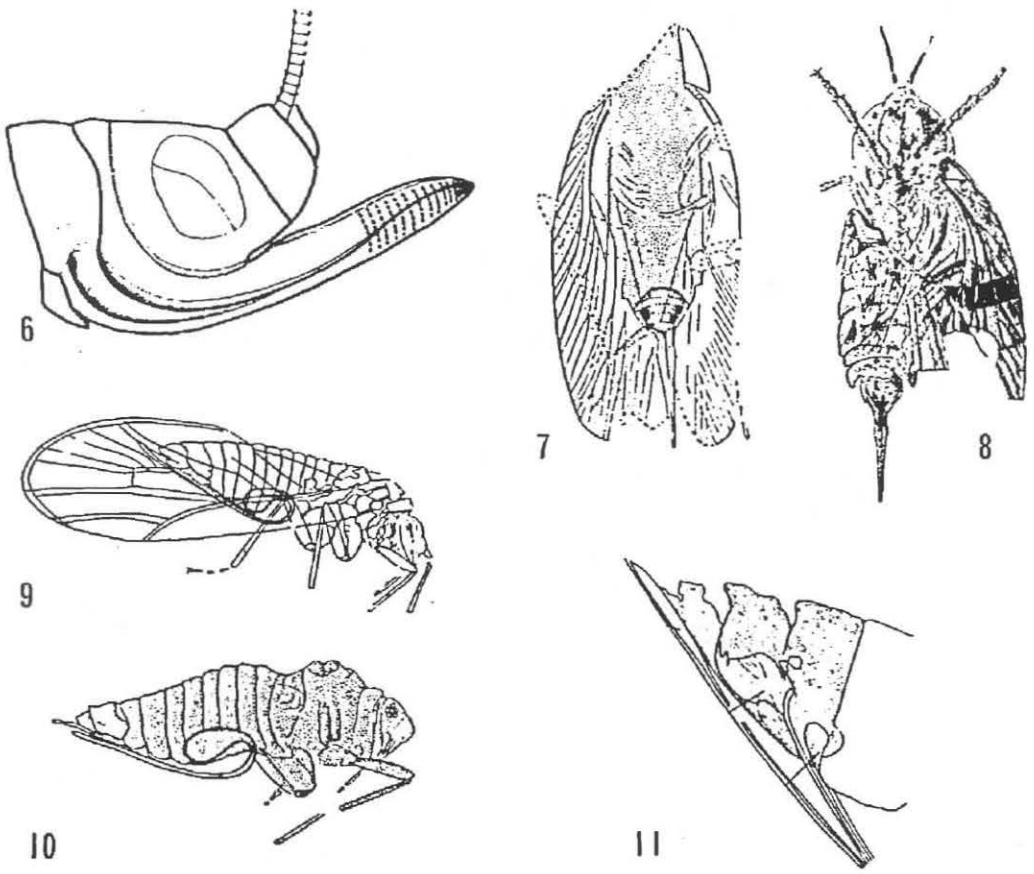


FIG. 6. Drawing of distal part of abdomen of *Asthenohymen dunbari* Tillyard (Diaphanopterodea), from Lower Permian of Kansas; original drawing by Dr. J. Kukalová, based on specimens in Museum of Comparative Zoology.

FIG. 7. Drawing of *Uraloblatta insignis* Zalessky (Blattaria) from Permian of Urals, USSR, showing ovipositor (from Zalessky, 1939).

FIG. 8. Drawing of *Kunguroblattina microdictya* Becker-Migdisova and Vishniakova (Blattaria), from Permian of Barda, near Perm, USSR, showing ovipositor (from Becker-Migdisova, 1962).

FIG. 9. Drawing of *Archescytina* sp. (Hemiptera) from Permian of Tshekarda, USSR, showing ovipositor (from Becker-Migdisova, 1960).

FIG. 10. Drawing of *Archescytina* sp. (Hemiptera) from Permian of Tshekarda, USSR, showing ovipositor (from Becker-Migdisova, 1960).

FIG. 11. Drawing of *Archescytina* sp. (Hemiptera) from Permian of Tshekarda, USSR, showing detail of ovipositor (from Becker-Migdisova, 1960).

variety of superfamilies which have existing representatives (Becker-Migdisova, 1961; Evans, 1956). The significance of this large array of hemipterous insects in the Paleozoic is obvious: there must have been abundant sources of liquid plant food available. With the Palaeodictyoptera, Megasecoptera and Diaphanopterodea also present, it is perhaps not an exaggeration to state that nearly half of the species of Paleozoic insects had piercing-sucking mouthparts. (The account by Baker and Hurd [1968, p.

386] of the early development of feeding mechanisms in the insects is obviously contrary to the actual geologic evidence.)

OVIPOSITORS

A different type of adaptation well established in the Upper Carboniferous and Permian insects was development of a prominent, exserted ovipositor in the females. An ovipositor of some sort, varying from slight extensions of parts of the eighth or ninth abdominal sternites to several pairs of long valve-like processes, occurs in many groups of living insects. Of special interest are those with the long ovipositors, used for depositing eggs in plant tissue, soil, or animal hosts. Such ovipositors have been developed independently many times; they occur, for example, in some Neuroptera (Dilaridae and Raphidiodea), in most Hymenoptera and in many Orthoptera (Saltatoria). In neither of the two existing orders of Paleoptera, the Ephemeroptera and Odonata, is the ovipositor long or well developed as in the insects just mentioned.

Studies that have been made in recent years on the Upper Carboniferous and Permian Palaeodictyoptera, Megasecoptera and Diaphanopterodea have shown that in all of these the ovipositor was very well developed, resembling that present in some of the Saltatoria in general form, though presumably not in detailed structure. The presence of such ovipositors (Fig. 6) in these groups strongly suggests that the immature stages of these particular insects were not aquatic, as are the nymphs of Odonata and Ephemeroptera. The adults presumably deposited their eggs in the particular environment in which the young insect would develop and it is most unlikely that the long ovipositor in the adult would be an adaptation for depositing eggs under water. As is well known, some adult odonates do enter water and deposit eggs on the surface of submerged plants or in cuts in the plants made by small ovipositors. However, the long ovipositors in these three extinct orders do not seem to have been an adaptation for oviposition in the aquatic environment; much more probable would be deposition of eggs in either soil, decaying vegetation or plant tissue.

Since many Recent Orthoptera (Saltatoria) have long ovipositors, it is not surprising to find that Paleozoic members of the group had similar structures. Saltatorial Orthoptera with such ovipositors have been found in the Upper Carboniferous shales of Commentry in France, as well as in Permian deposits of the Soviet Union. What is surprising, however, is the presence of equally long ovipositors in Paleozoic cockroaches (Blattaria) (Figs. 7, 8). Apart from a few viviparous roaches, Recent species deposit their eggs in an egg-case (ootheca), which could not conceivably be done with the long and slender ovipositors of the Paleozoic members of the order. It is indeed unexpected, as has been demonstrated so well by Vishniakova (1968), that elongate ovipositors were present even in Jurassic roaches, although in some the ovipositors were relatively short.

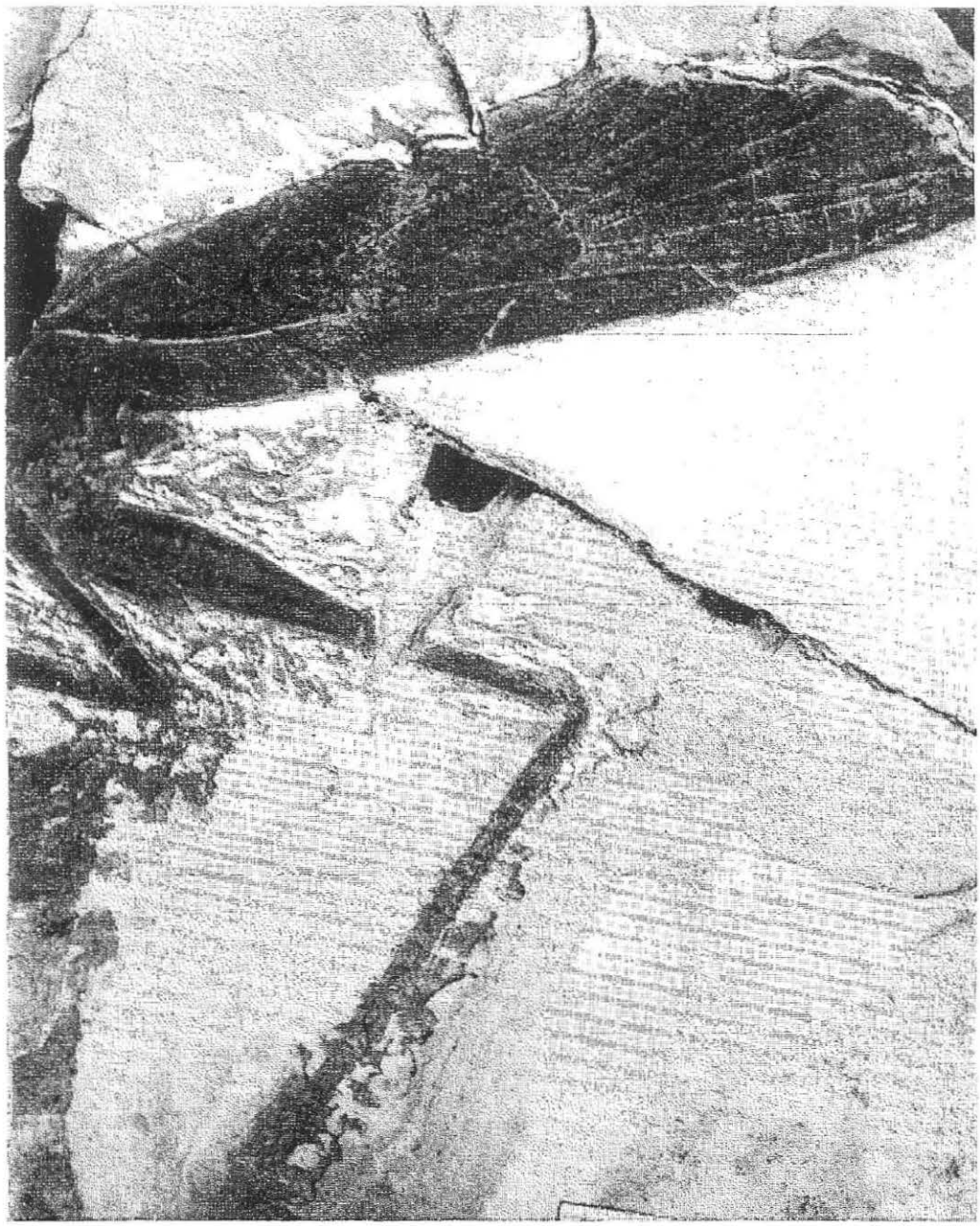


FIG. 12. Photograph of *Oedischia williamsoni* Brongniart (Orthoptera), from Upper Carboniferous of Commentry, France; original photograph of type specimen in Institut de Paléontologic, showing forewing and the modified hind leg.

The occurrence of egg laying by oothecae in both the Blattaria and the Manteodea has been considered by several entomologists as indicative of a close phylogenetic relationship between these two orders. However, the presence of the long ovipositor in Paleozoic roaches is strong evidence that development of oviposition by oothecae was independently attained in these two orders. Whatever the circumstances were at the time and place of

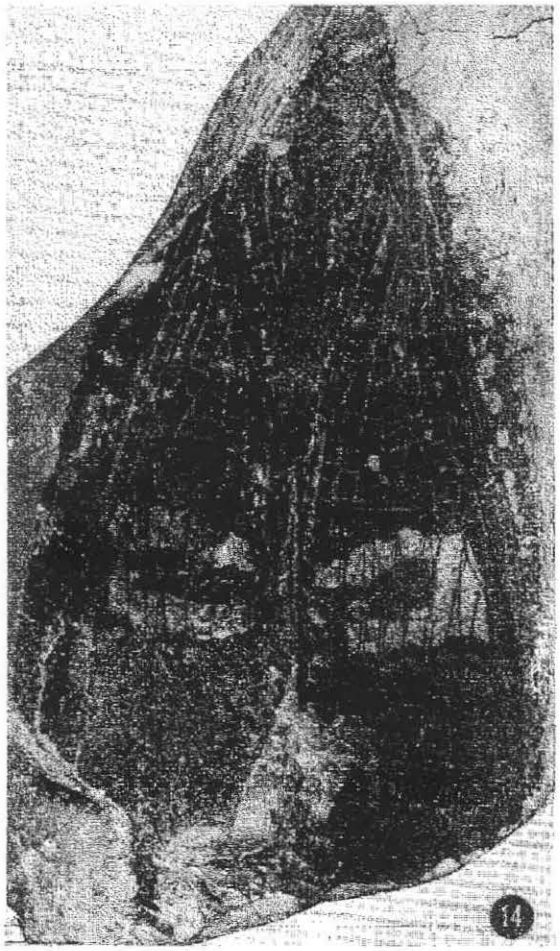


FIG. 13. Photograph of *Protodiamphipnoa tertrini* Brongniart (Protorthoptera), from Upper Carboniferous of Commentry, France; original photograph of specimen in Institut de Paléontologie, showing the raptorial front legs. The large spines on the femur and tibia do not show up well in this specimen but are clear in others.

FIG. 14. Photograph of another specimen of *Protodiamphipnoa tertrini*, showing the eye-spot marking on fore wings; original photograph of specimen in Institut de Paléontologie, from Upper Carboniferous of Commentry, France.

existence of these Paleozoic and Jurassic roaches, it seems clear that eggs must have been laid singly and deposited to a considerable depth in soil, organic debris or soft plant tissue.

In this same connection, I wish to call attention to the unexpected presence of long ovipositors in Permian Homoptera. These were noted many years ago in Lower Permian forms (Carpenter, 1939, pl. 1, fig. 3) but not until recent years, after numerous specimens were found in many positions, did the nature of these structures become clear. As shown in the accompanying illustration (Figs. 9, 10, 11) the ovipositor was not only long but it was coiled up beneath the abdomen of the insect when it was retracted. Although there are a few Homoptera which now have recognizable ovipositors, none have long ones like those found in such Permian forms.

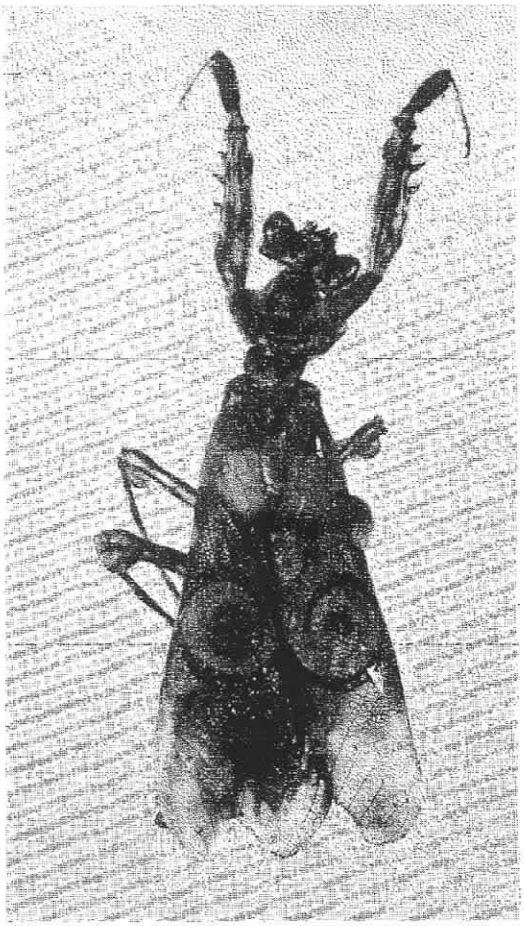


FIG. 15. Photograph of *Pseudocreobotra ocellata* Saussure (Manteodea), from Africa (Recent); original photograph of specimen in the Museum of Comparative Zoology, showing eyespots on the fore wings. Compare with Figs. 13 and 14.

LEGS

The legs of Paleozoic insects were clearly adapted for several specialized activities. The usual and presumably valid assumption is that the legs of insects were originally cursorial, that is, adapted for walking. In at least two orders of Carboniferous insects, Protodonata and Protorthoptera, the front legs were modified for grasping and holding prey. In the protodonates, as in the odonates, the legs were armed with stout spines, which obviously aided in holding victims. In some Protorthoptera, which appear to have no close ordinal affinities with the manteids ("praying mantis"), the front legs were elongate and obviously raptorial (Figs. 13, 14) (compare with Fig. 15). Of special interest also is the modification of the hind legs for leaping (Fig. 12). This is found in certain Carboniferous insects (Oedischiidae) which were apparently closely related to the insects we now recognize as grasshoppers and their relatives (order Orthoptera). It is an interesting adaptation to find in Carboniferous insects because of its limited occurrence among

living species. The advantage of jumping legs to a flying insect is not clear; probably they enabled the insects to take flight from a region of compact vegetation and thus to escape more readily from potential danger.

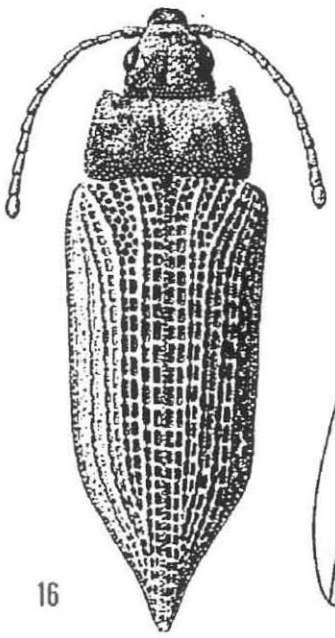
WINGS

The wings of Paleozoic insects are remarkable in their diversity and in their specializations. Indeed, the development of wings in the insects, at least by the beginning of the Upper Carboniferous, was a unique achievement, flight not being attained by vertebrates until the Jurassic. Furthermore, the wings of insects were not modified legs or homologous appendages, as in flying vertebrates, but were apparently developed as new outgrowths of the body wall. What we find on examining the wings of the Upper Carboniferous and Permian insects is that in many cases they show more extreme modifications than in related groups of the present day. For example, some early Permian damselflies (order Odonata, suborder Zygoptera) have the wings even more petiolate than those in any Recent species of the order. In their most primitive condition, the fore and hind wings were alike or essentially so (homonomous). In most of the Palaeodictyoptera, Megasecoptera and Diaphanopterodea this was the case, but in at least three families of Palaeodictyoptera the hind wings were reduced in size and in a few forms apparently they were completely lost (see Kukalová, 1970a). A similar sequence of events occurred in the history of the mayflies (Ephemeroptera) in the course of their development from Upper Carboniferous to present time.

The tendency for the hind wings to become expanded, with complicated patterns of folding, is visible in most living neopterous insects. Similarly enlarged hind wings were present in Upper Carboniferous Neoptera, such as the Blattaria and Protorthoptera.

Modification of the front wings into thickened covers or elytra apparently occurred at least twice among Permian insects. One of these occasions was in the extinct Protelytroptera, an order known only from the Permian, in which the fore wings range in some families from flat, tegminous structures with a well-developed venation, to strongly convex and thick elytra, in which the venation is nearly lost (Carpenter, 1933) (Fig. 17). Coleoptera, with well-developed elytra, are also known as far back as Permian (Fig. 16). The similarity between the elytra of some Protelytroptera and some Coleoptera is very striking, but the hind wings are very different in the two groups (Carpenter and Kukalová, 1964). On the basis of information now available, the Protelytroptera seem most likely to have been close relatives of the Blattaria or some other orthopteroid group. At any rate, modification of the front wings to elytra, presumably defensive structures, was clearly attained by insects at least as far back as the early Permian.

Insect wings from the Upper Carboniferous and Permian show a number



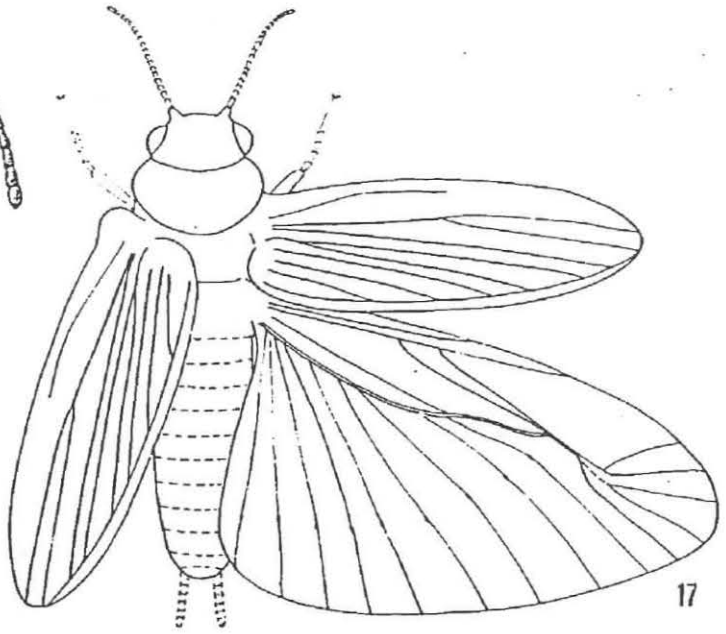


FIG. 16. Drawing of *Permocupes sojanensis* Ponomarenko (Coleoptera), from Permian of Arkhangelsk Region, USSR (from Ponomarenko, 1969).

FIG. 17. Drawing of *Protelytron permianum* Tillyard (Protelytroptera), from Lower Permian of Kansas; based on specimens in Museum of Comparative Zoology.

of venational and other structural devices reminiscent of those which occur among different and unrelated groups of living insects. At present we do not have a clear understanding of many aspects of the dynamics of the insect wing. However, if we examine a series of wings of different orders of insects we note that there is a recurring tendency for strengthening of the wing membrane by transverse struts at about one-quarter to one-third the wing length from the base. This has been achieved in various ways. In Odonata, for example, the common stem of the radial sector and the media diverges away from its more basal, longitudinal position and assumes an oblique position (arculus) near the basal part of the wing; this is further strengthened by the presence of additional strong cross veins that eventually form a series of triangles or quadrilaterals in that part of the wing. It is interesting to find that in such extinct orders as the Palaeodictyoptera similar tendencies for the strengthening of the same areas can be seen. By way of comparison, in the family Calvertiellidae there are complicated modifications of the veins in that region of the wing which result in a structure quite comparable to what we find in the Odonata (Kukalová, 1968). Study of the precise veins shows that the parts of these two types of supporting structures are not at all homologous.

The final aspect of the wings of Paleozoic insects which I wish to mention is wing markings. Most insects now living, especially those in which the wings are membranous, have markings in the form of spots or bands or a

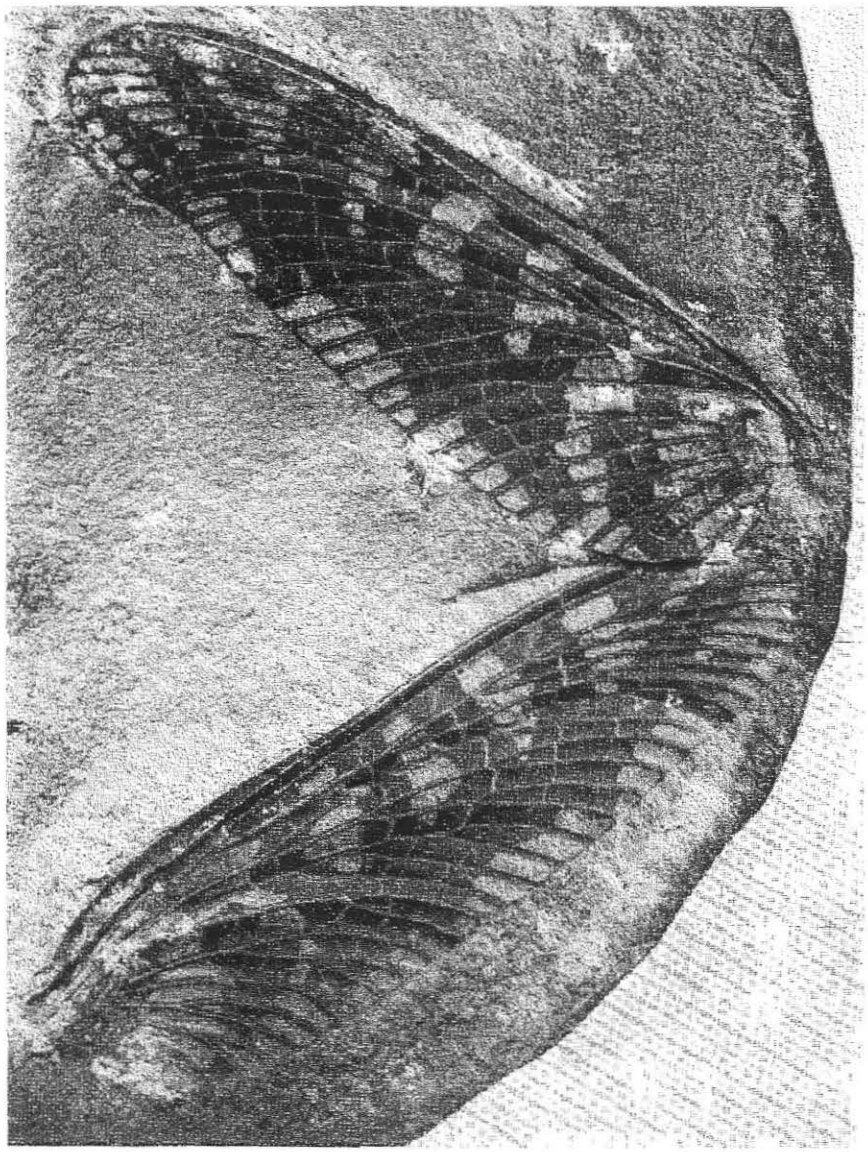


FIG. 18. Photograph of *Homaloneura dabasinskasi* Carpenter (Palaeodictyoptera), from Upper Carboniferous of Illinois; original photograph of type specimen, showing wing markings.

combination of these two, distinguishable by contrasting colors. Although we are unable to determine the original color of the markings in fossil insects, the presence of such markings is indicated in especially well preserved specimens by varying intensities of black or brown pigmentation (Figs. 18, 19, 20). The process by which these markings have been preserved in the fossils is by no means clear; it has been observed that exposure of such specimens to bright light, such as sunshine, results in a gradual fading and final complete disappearance of the maculations in the fossils. Nevertheless, there can be no question that these were actual maculations and not artifacts, since the markings are the same in the several specimens of one

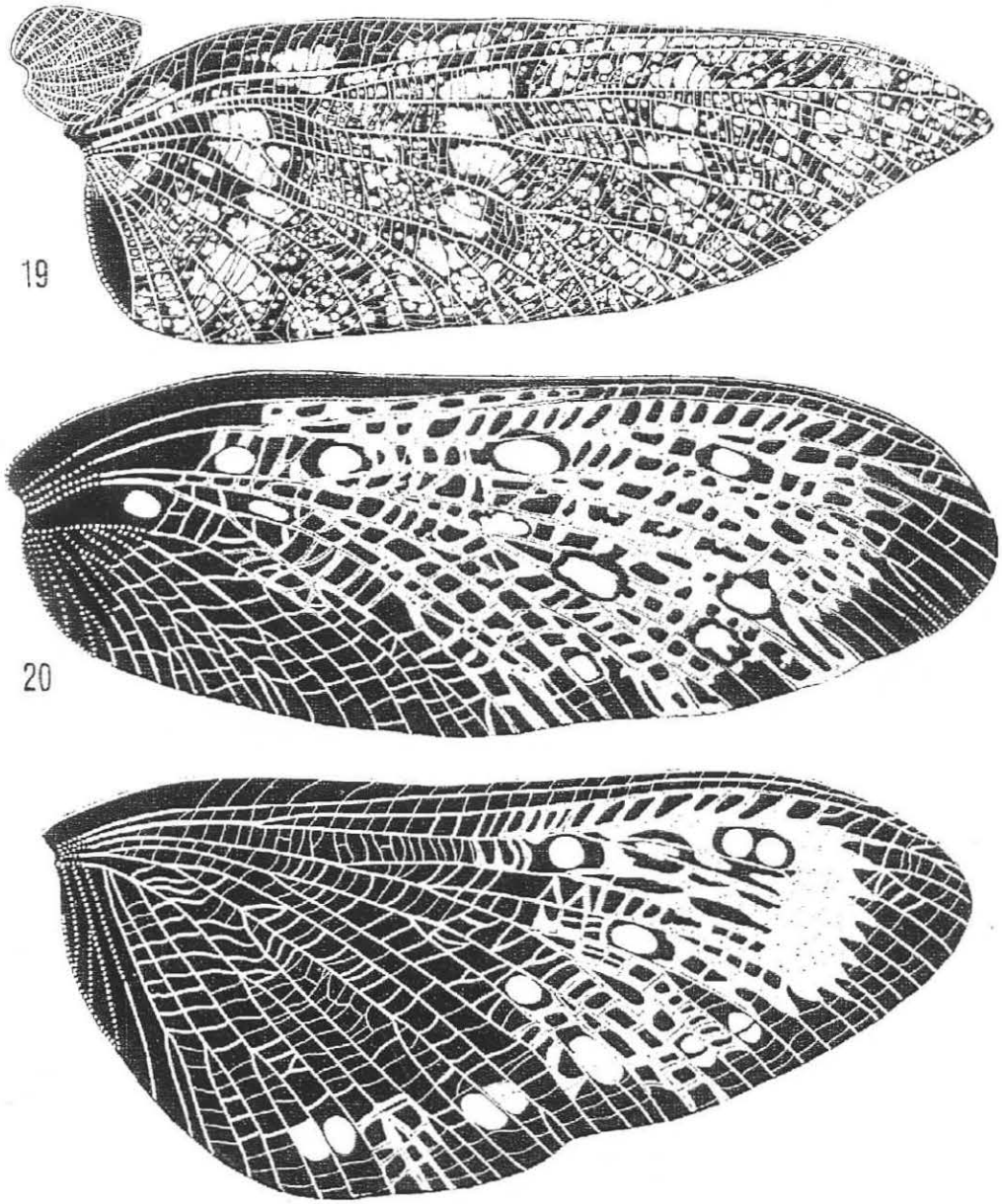


FIG. 19. Drawing of fore wing and prothoracic lobe of *Homoioptera gigantea* Agnus (Palaeodictyoptera), from Upper Carboniferous of Commentry, France; original drawing by Dr. J. Kukalová, based on type specimen in Institut de Paléontologie, Paris, showing delicate maculations.

FIG. 20. Drawing of fore and hind wings of *Lamproptilia grandeuryi* Brongniart (Palaeodictyoptera), from Upper Carboniferous of Commentry, France; original drawing by Dr. J. Kukalová, based on type specimen in Institut de Paléontologie, Paris, showing maculations on both wings.

species. An example of this is furnished by the dozen or more specimens of *Dunbaria fasciipennis,* a palaeodictyopteron from the Lower Permian of Kansas, showing distinctive color bands across the wing.

The degree of diversity of wing markings in Paleozoic insects is indeed

striking, especially in the case of those from Upper Carboniferous deposits. In the Palaeodictyoptera, markings vary from minute spots, covering almost the entire wing surface, to broad bands that apparently line up across from the fore wing to the hind wings, as is usually the case in living insects with such markings. A striking example of this is *Homaloneura dabasinskasi,* from Pennsylvanian nodules near Mazon Creek in Illinois (Fig. 18). It is quite possible that such wing markings might well have been involved in species recognition, during courtship behavior of these early insects.

Of special interest is the presence of unquestionable eye-spots on the wings of one Upper Carboniferous species, *Protodiamphipnoa tertrini,* from Commentry. Such markings in Recent insects are generally considered to be deterents, which might frighten predators or disturb the accuracy of an attack. The eye-spot in the fossil mentioned occurs only on the fore wings (Fig. 14), which were held back over the body at rest; it is very much like that eye-spot found in some orthopteroids at the present time (Fig. 15). Whether this was a defensive device in *Protodiamphipnoa* or one of sexual recognition we cannot determine, but it is another instance of modifications in Paleozoic insects similar to those occurring in some present day groups.

SUMMARY

The foregoing examples are sufficient to show that insects of the Upper Carboniferous and Permian periods were highly adapted to various types of food and predation. A higher percentage of the orders of Upper Carboniferous insects, for example, apparently had their mouthparts adapted for piercing and for sucking up liquid food than in the existing fauna; a high percentage of them obviously had long, exserted ovipositors for depositing eggs in particular and specific environments; the legs were modified for grasping prey, for running or for leaping; and the wings elaborately developed as organs of flight or as protective covers. In addition, we might well conclude that Carboniferous and Permian insects were as colorful as those at the present time, even though we have no idea what those colors might have been. Indeed, it seems most likely that insects of the Carboniferous and Permian were just as highly adapted to their particular types of environments as existing insects are to theirs.

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